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ADDITIONAL FINDINGS ON THE MORPHOLOGY OF THE PROXIMAL PART OF THE REPRODUCTIVE SYSTEM OF THE STYLOMMATOPHORA (GASTROPODA, PULMONATA)

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ABSTRACT

The external, internal, and histological structure of the fertilization-pouch-seminal-receptacle complex (FPSC) was studied. Great structural variation was found in the FPSC, both in the form and size of the chambers, and in the presence of spermathecal pouches and the fertilization chamber. It is very probable that, upon studying a greater number of specimens, it will be possible to use the characters of the FPSC for systematic purposes. It was shown that oogenesis usually occurs in the time period from April to July; beginning in August, spermatogenesis prevails.

INTRODUCTION

The details of the structure of the reproductive system of many representatives of pulmonate land mollusks (Stylommatophora) are more or less completely described in the works of many authors. Special attention has been paid to the distally placed organs and appendages, as they hold an important meaning for classification. The structure of the proximal parts of the

reproductive system -- the region lying between the spermoviduct and the gonads, especially the fertilization-pouch-seminal-receptacle complex (the FPSC) -- have been poorly studied.

Besides the gonad with the hermaphroditic duct, the proximal section of the reproductive system contains two more structures: the albumen gland and a complicated system that will be called the FPSC (Fig. 1). In the naming of organs there is no uniformity, and this is why in the beginning it is necessary to clarify the terms of separate elements in relation to their functions.

Typically, the FPSC chamber appears to be a specialized part of the distal region of the hermaphroditic duct (where the duct joins with the canal of the albumen gland). This specialized unit is located on a more or less sharp bend of the hermaphroditic duct, submerged to varying degrees within the tissue of the albumen glands and usually differentiated into two chambers, the form and sizes of which are extraordinarily variable. One of these chambers is the actual fertilization pouch (Befruchtungstasche, fecundation pouche), the second serves for storage of the sperm of the partner (allosperm), that have entered from the spermatheca (bursa copulatrix, receptaculum seminis, gametolytic gland). Thus inside the body of the mollusk there exist two places for allosperm: the distal, where the sperm end up directly after copulation, and the proximal, which receives a portion of the allosperm after a certain period of time following copulation. Traditionally, we call the distal

storage area the spermatheca, and the proximal chamber the seminal receptacle, even though both terms carry the same meaning. The seminal receptacle contains the sperm that is physiologically ready for the fertilization of the egg. Fertilization occurs in the adjacent fertilization pouch.

The confluence of the ducts that descend from the spermatheca and the albumen gland is commonly called the carrefour (Bayne 1973), which literally means crossroads, or intersection. The complex as a whole (the distal part of the hermaphroditic duct, or the ascending duct + fertilization pouch + seminal receptacle + descending duct), in foreign literature, goes under the uncertain term of "talon." The meaning of the term FPSC should be expanded; by this term we signify the whole complex that has a morphological and functional unity. The term "fertilization pouch" is the accepted one in Soviet scientific literature, which we will use only to describe just one part of the complex (FPSC). The fertilization pouch is joined with the seminal receptacle through an opening, which we suggest calling the "fecundatory pore" (fecundus = fertilizing).

Initially, the internal structure of the FPSC of a representative of the higher order of the Stylommatophora--_Helix pomatia_--was described in the works of Meisenheimer (1907, 1912) and later, this description was included by Kilias (1960) in a popular treatment of the common vineyard snail. Recently, Lind (1973) corrected and verified the data of Meisenheimer. In essence, the findings of these authors exhaust our knowledge of

the morphology of the FPSC of the higher Stylommatophora. Flasar (1967) devoted special work to the study of the FPSC of Oxychilus draparnaudi (Zonitidae). He emphasized the great variation in this structure among the studied species and the common vineyard snail. However, these differences mainly involve the shape of both chambers, and are of little value to systematics. Van Mol (1971) analyzed FPSC morphology in detail for some Bulimulidae, and showed that the FPSC in representatives of this family is long, and that the fertilization pouch is small, but that there is a gigantic seminal receptacle, that consists of a number of tubular pouches. In mollusks of the family Succineidae, both compartments of the FPSC are small, compact, and easily seen during external examination (Bayne 1973). Without going into great detail, investigators have noted differences in the external appearance of the FPSC among many groups of mollusks: for example Steenburg (1925) and Wiegmann (1901) in the lower stylommatophoran order Orthurethra (Pupillidae, Enidae), and Pilsbry (1939-1946) in representatives of the more numerous families that inhabit North America.

We studied the external view and the internal structure of 63 species from different families of the Stylommatophora and the histological structure of the FPSC of 17 species of the Helicoidea to find characters that might be useful for systematics.

METHODS

The mollusks were dissected, the FPSCs were extracted and cleansed of tissue of the albumen gland and were then clarified in glycerine. To arrive at a general understanding of the internal structure of the FPSC, several cross-sections were made at different levels using ophthalmic scissors. For histological investigation the FPSC was sectioned together with the adjacent parts of the spermoviduct, albumen gland, and hermaphroditic duct. Samples were fixed in 70% ethyl alcohol; prior to fixation the animals were drowned in water for a period of 18-24 hours. Before immersion in paraffin, butanol was used. The series of cross-sections, each with a thickness of seven microns, was stained with hematoxylin and with eosin or orange G.

RESULTS

Morphology of the FPSC

Primitively the FPSC, as mentioned above, is a slightly differentiated part of the hermaphroditic duct. In some Orthurethra (for example _Partula otaheitana_ and some Enidae) we were unable to find two chambers in the corresponding part of the hermaphroditic duct. The development and partitioning of the FPSC can already be observed in some Orthurethra; in many Enidae and Pupillidae the FPSC is externally manifested very clearly; often, even during external examination, the two chambers can be seen. Representatives of the family Tornatellinidae deserve particular mention, especially the genus _Fernandezia_, in which

the length of the FPSC exceeds half the length of the uterus; moreover the FPSC is rather superficially connected with the albumen gland. The internal structure of the FPSC of these mollusks, unfortunately, has not been studied. In the majority of the Orthurethra, the upper part of the hermaphroditic duct within the limit of the albumen gland contains a transverse fold; apparently this fold is the precursor of the FPSC. All the other investigated Stylommatophora have an FPSC consisting of two chambers, an ascending duct, and a descending duct, but the structure of these chambers in mollusks of different groups is significantly complicated by the presence of various appendages, or pockets. More often than not, the pockets are formed in the seminal receptacle, less often in the fertilization pouch. The most developed pockets of the seminal receptacle occur in some species in the families Bulimulidae and Oreohelicidae. In these taxa, the seminal receptacle achieves a great length and is hardly imbedded in the tissue of the albumen gland at all; moreover, in the Oreohelicidae, the seminal receptacle is considerably pigmented (intensely black) and tightly wound in a spiral.

External and internal variation of the FPSC in the Helicoidea is substantial (Fig. 2). In some cases the FPSC seems diagnostic of most members of a particular genus, family, or subfamily. However, the extent of studied material is inadequate to determine the systematic significance of the morphology of these organs. A characteristic structure of the FPSC has been

noted in the Polygyridae. In this family, the expanded pockets of the fertilization pouch are adjacent to most of the short, spherical pockets of the seminal receptacles, giving the apical end of the FPSC a nodular appearance. Some similarity to this appearance is observed in the Helicodontidae; however, in species of this family the fertilization pouch is only weakly developed. The Bradybaenidae are characterized on the whole by relatively long ascending and descending ducts along with quite short and closely appressed fertilization pouch and seminal receptacle. In the majority of the Hygromiidae, the FPSC on the whole is short and wide, with one to three pockets extending from the fertilization pouch, which is quite often positioned across from the seminal receptacle.

By studying 17 species in great detail, we can formally combine them into four groups according to the structure of their FPSC: 1) fertilization pouch and seminal receptacle both simple and without pockets (Xerosecta crenimargo, Bradybaena stoliczliana, Bradybaena fruticum); 2) fertilization pouch with pockets but seminal receptacle simple (Hesseolo solidior, Trichia hispida, Archaica heptapotamica, Archaica sp., Leucozonella sp.); 3) fertilization pouch simple but seminal receptacle with pockets (Oreohelix strigosa, Lindholmiola corcyrensis, Perforatella bidens, Pleurodonte isabella); 4) fertilization pouch and seminal receptacle both with pockets (Caucasigena abchasica, Ammonitella yatesi, Leucozonella rufispira, Webbhelix multilineata, Xeropicta candaharica).

The purpose of these artificial groupings is to present our meager findings in an organized way. It should be noted that the species included in any of these groups are significantly different. For example, in the third group, which includes four species belonging to four families (Oreohelicidae, Helicodontidae, Hygromiidae, and Camaenidae) we can observe four distinct morphologies of the FPSC connected only by a superficial similarity in the presence of pockets in the seminal receptacle. In _Oreohelix strigosa_, the seminal receptacle consists of two multipocketed clusters joining into two ducts. The seminal receptacle of _Lindholmiola corcyrensis_, on the contrary, is nodular, almost spheroidal, with several very short pockets in the form of indentations. In _Perforatella bidens_ the seminal receptacle has three pockets ending on different levels. Finally, in _Pleurodonte isabella_ the whole length of the seminal receptacle is separated by one barrier into two narrow pockets of different length.

The diversity in structure of the FPSC enables us to hope that it can be used for systematics. Exactly which characters can be used and on what level can be determined only after the investigation of the majority of species in each family.

Histological Structure of the FPSC

The hermaphroditic duct in the region of its ascending duct is distinct from its gonadal section, where there are seminal vesicles in different developmental stages. The wall of the

ascending duct externally consists of ringlike muscle fibers alternating with elastic fibers; and in some cases the latter prevail. The internal surface of the canal is pleated and lined with a ciliated columnar epithelium. The cytoplasm of the epithelial cells is viscous and the apical part is filled with granules.

The combination of cilia and muscles suggests that this section actively transports spermatids and eggs to the FPSC. The pleated structure of the walls leads us to think that spermatids arrive in groups and upon arrival of each group, the duct expands in diameter by unfolding the longitudinal pleats. Most likely, upon the arrival of a group of spermatids the ring-like muscle mass is first to act, creating peristalsis. The cilia provide mostly for the transport of the female gametes. In several species the hermaphroditic duct, directly upon joining the fertilization pouch, forms one to three pockets. In <u>Xeropicta candaharica</u> fixed during the winter under laboratory conditions these pockets as well as the fertilization pouch were filled with spermatozoids.

The walls of the descending duct and the fertilization pouch also consist of ringlike muscular and elastic fibers. In several species (<u>Oreohelix</u> <u>strigosa</u>, <u>Xeropicta</u> <u>candaharica</u>, <u>Xerosecta crenimargo</u>) these contain pigment cells, which stain, sometimes very intensely, all of the FPSC and especially the fertilization pouch. The internal surface of the walls is pleated and lined with ciliated columnar epithelium. In the areas of the pleats a

false impression of a multi-layered epithelium can be formed due to the overlapping of cells. In several species (e.g. Ammonitella yatesi) sperm were discovered in the lumen of the descending duct. In histological structure, the walls of the seminal receptacle and the descending duct differ from those of the fertilization pouch if the seminal receptacle is long and partitioned into many parts, e.g. consisting of many pockets. In this case, the ciliated epithelium of the apical part of the seminal receptacle consists of cubic cells which gradually transform into columnar. The external layer of the wall of the seminal receptacle also loses many of its elements (except for the pigment cells) as a result of its branching and the decreasing diameter of its pockets.

Judging from this, we hypothesize that the seminal receptacle functions as more than just a container for allosperm. Spermatids spend a period of physiological maturation inside the seminal receptacle in close contact with separated epithelial cells which, under these circumstances, lose cilia (Van Mol 1971).

Seasonal Changes in the Gonad and the FPSC of Trichia hispida

Collections of this species were made near Moscow in April, May, June, July, August, and November. Depending on the season, we noted drastic changes in the volumes of the hermaphroditic duct and the albumen gland. A more dramatic difference was observed among individuals collected in July and August (Fig. 3).

Similar differences were observed in all species for which we were able to collect seasonal data (Schileyko, 1971). Obviously, there is a close relationship between certain seasonality and the prevalence of spermatogenesis or oogenesis.

Histological analysis confirmed this hypothesis. From April until July, oogenesis could clearly be observed in the gonad. The tissue structure of the walls of the ascending duct and FPSC become more dense, and the epithelial cells which line the internal surface are extended inward toward the lumen; the lumen of the duct decreases but the lumen of the secretory canal of the albumen gland, like the gland itself, is dramatically enlarged. In an individual collected in May, an egg was found in the fertilization pouch. From the end of July until August the morphology changes quickly: spermatogenesis dramatically takes over, the walls of the gonad get thin, and the lumen of the gonad enlarges. A snail fixed in November, in a state of winter hibernation, bears a large resemblance to the one found in April; but eggs were found in its gonads.

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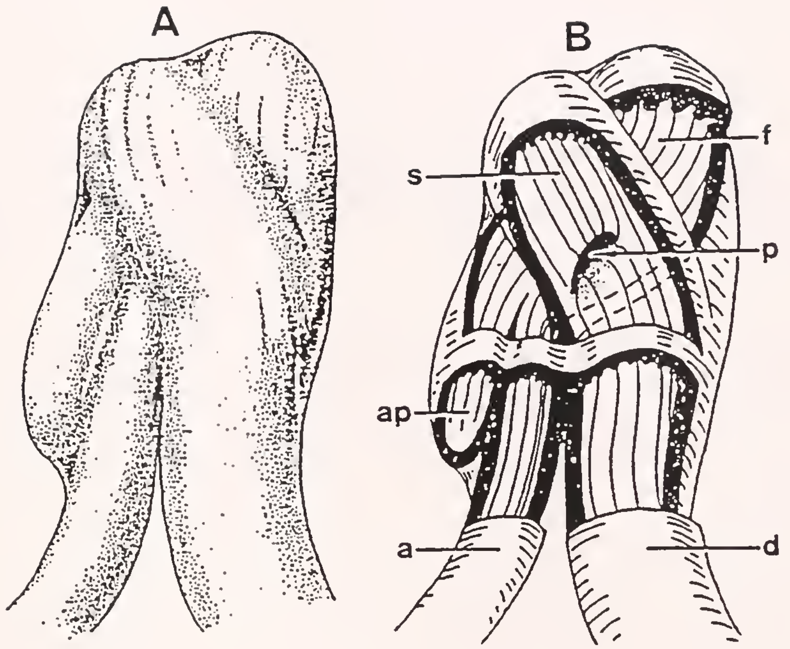

Fig. 1. External view (A) and internal structure (B) of the FPSC of Fruticocampylaea narzanensis.

a = ascending duct (distal hermaphroditic duct); ap = pocket of ascending duct (= pocket of fertilization pouch); d = descending duct; f = fertilization pouch; p = fertilization pore; s = seminal receptacle

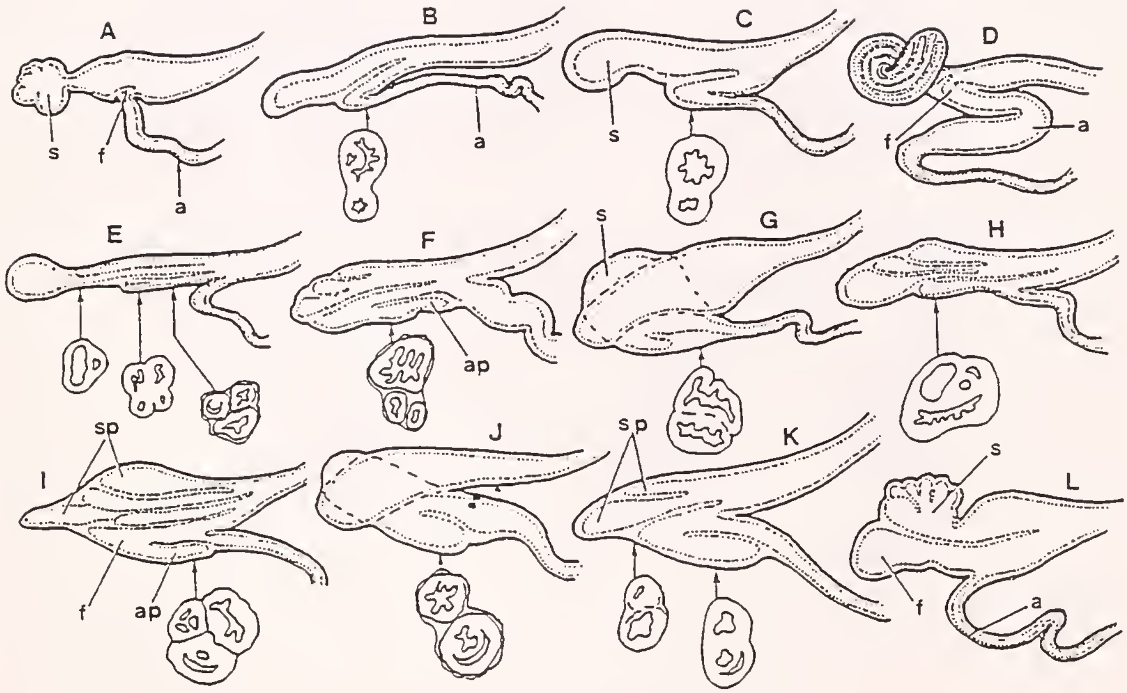

Fig. 2. External view and the internal structure of the FPSC of various representatives of the Helicoidea. A. Lindholmiola corcyrensis; B. Bradybaena fruticum; C. Xerosecta crenimargo; D. Oreohelix strigosa; E. Pleurodonte isabella; F. Leucozonella rufispira; G. Archaica heptapotamica; H. Perforatella bidens; I. Xeropicta candaharica; J. Hesseola solidior; K. Karabaghia bituberosa; L. Triodopsis multilineata.

a = ascending duct (distal hermaphroditic duct); ap = pocket of ascending duct (= pocket of fertilization pouch); f = fertilization pouch; s = seminal receptacle; sp = pockets of seminal receptacle

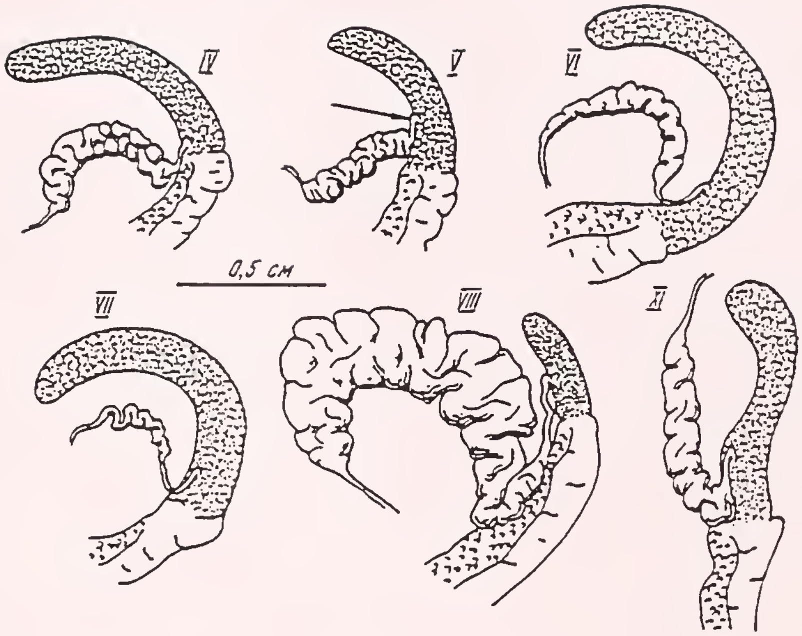

Fig. 3. External view of the albumen gland and the hermaphroditic duct of Trichia hispida in different seasons. Roman numerals indicate months. The arrow indicates the position of the FPSC.